

CHAPTER 10: CROSS-TAXONOMIC PATTERNS OF DIVERSITY

RESULTS

Alpha Diversity

Three of the five taxonomic groups sampled in this study were described at the species level, including birds, mammals, and vascular plants. Among these three groups, vascular plants were most speciose, followed by birds and mammals (Table 171). Invertebrates and fungi were described at the family and genus level, so their richness values can not be compared directly to that of birds, mammals, and vascular plants. However, the over 200 invertebrate families encountered are estimated to easily represent 3 to 4 times that many species. Given that few species of macrofungi per genus are suspected to occur in the basin, the 55 macrofungi genera are unlikely to exceed 150 species.

TABLE 171. Taxonomic groups and their richness in the study area.

Taxonomic group	Taxonomic level	Number of taxa
Birds	species	101
Mammals	species	35
Invertebrates	family	203
Vascular plants	species	470
Fungi	genus	55

Relationships Among Taxonomic Groups

Animal Group Interrelationships

Among the 3 animal groups, only changes in the richness of birds and invertebrates were significantly correlated (Table 172). Bird species richness was significantly positively correlated with invertebrate family richness ($r = 0.205$, $P = 0.069$) (Fig. 64). Birds and invertebrates both had positive relationships with meadow and lodgepole pine, including a positive correlation with the forest to meadow gradient, and a negative correlation with channel gradient (Table 173).

TABLE 172. Correlations between the alpha diversity of 5 taxonomic groups. Bolded values indicate $P \leq 0.10$. Shading indicates redundant cells. Correlations between invertebrates and all other taxa were based on data collected in 1996 only, ($n = 56$ reaches), all other correlations were based on data collected in 1995 and 1996 ($n = 80$ reaches) in the Lake Tahoe basin.

Taxonomic group	Birds		Mammals		Invertebrates		Plants	
	r	P	r	P	r	P	r	P
Birds								
Mammals	-0.064	0.574						
Invertebrates	0.205	0.069	-0.071	0.531				
Plants	-0.274	0.014	0.186	0.098	0.102	0.366		
Fungi	-0.225	0.045	0.022	0.849	-0.279	0.012	-0.082	0.469

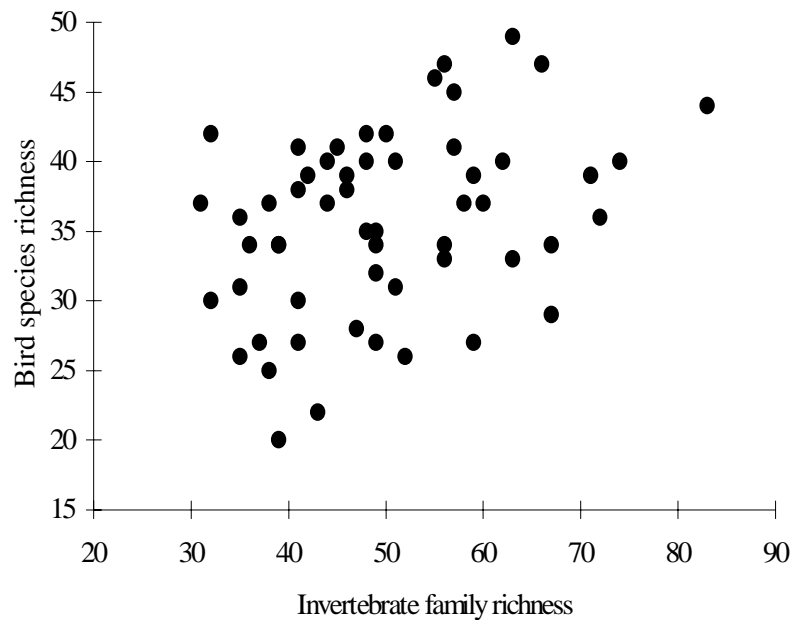


FIG. 64. Relationship between invertebrate family richness and bird species richness at sample reaches ($n = 56$) in the Lake Tahoe basin.

Animal, Plant and Fungi Interrelationships

Bird and mammal richness were both significantly correlated with plant species richness, with bird richness having a moderately strong negative correlation ($r = -0.274$, $P = 0.014$), and mammal richness having a significant but weak positive correlation ($r = 0.186$, $P = 0.098$) with plant species richness (Table 172, Fig. 65 and 66, respectively). Thus, sites rich in plant species also tended have a greater richness of mammal species and a lower bird species richness, however relationships were not strong enough to have any predictive value. Three reaches had particularly high plant species richness, but they did not appear to bias the correlations between plant richness and bird and mammal richness. These relationships were reflected in their respective relationships with the elevation–precipitation gradient (Table 173). It is likely that elevation and precipitation are the factors driving the observed relationships between plant species richness and both bird and mammal species richness. The positive relationship observed between mammal richness and plant richness was not as strong as the relationship observed for birds.

TABLE 173. Significant ($P \leq 0.10$) correlations between the richness of 5 taxonomic groups and environmental features as described by environmental gradients and individual variables. N = negative correlation, P = positive correlation. Bolded indicates $P \leq 0.05$. Blanks = non-significant correlations.

Environmental features	Taxonomic groups				
	Birds	Mammals	Invertebrates	Plants	Fungi
<i>Environmental gradients:</i>					
Elevation–precipitation	-0.393	0.273		0.240	0.201
Channel flow		-0.190			-0.346
Forest to meadow	0.402		0.238		-0.365
Subalpine vegetation					
Alder–willow			0.225	0.284	
Aspen–cottonwood	0.325	0.197			
Snag and log	-0.188				0.493
Channel log					
<i>Environmental variables:</i>					
Elevation	-0.313	0.364			
Precipitation	-0.337			0.341	
East				0.246	
West				-0.322	
Channel gradient	-0.376		-0.475		0.531
Channel sinuosity	0.199		0.233		
Channel width				0.233	
Mixed conifer			-0.400		0.189
Lodgepole pine	0.233		0.307	0.238	-0.204
Subalpine conifer	-0.304				0.222
Aspen–cottonwood	0.191	0.298			
Alder–willow			0.433		
Meadow	0.477		0.409	-0.248	-0.414
Canopy cover index					0.394
Large snag					0.468
Small snag					0.314
Large log	-0.212		-0.309	0.195	0.468
Small log	-0.210	0.265		0.245	0.289
<i>Total number of variables</i>	<i>10</i>	<i>3</i>	<i>7</i>	<i>8</i>	<i>10</i>

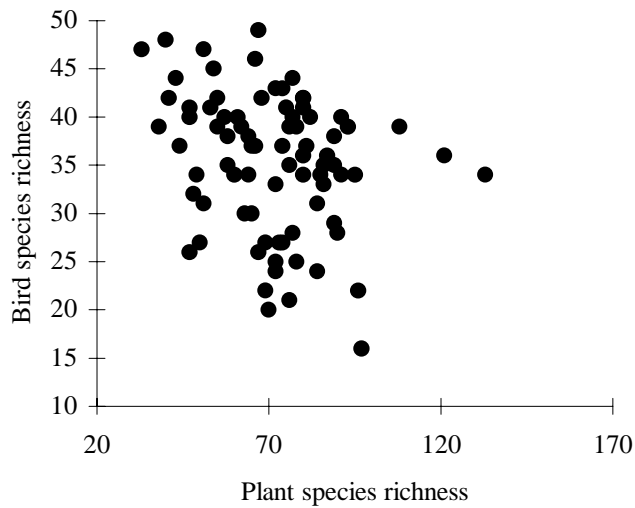


FIG. 65. Relationship between plant species richness and bird species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

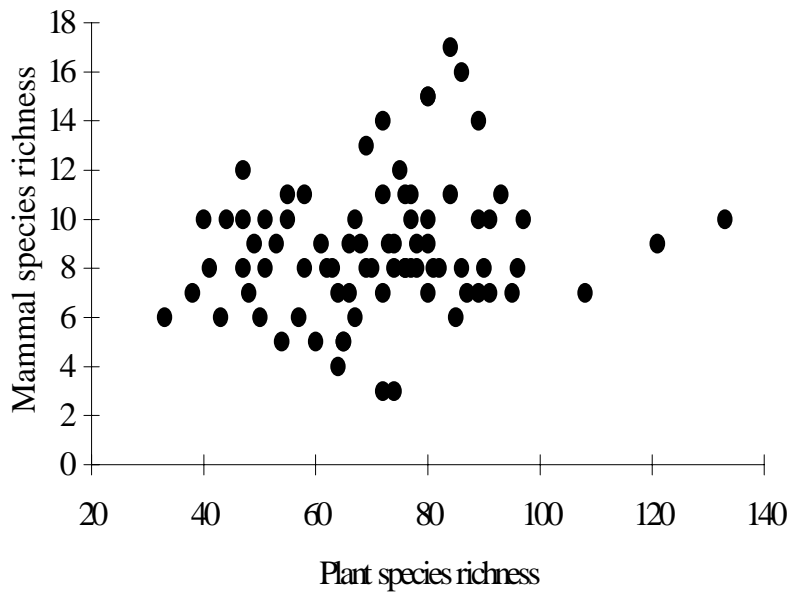


FIG. 66. Relationship between plant species richness and mammal species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

Bird and invertebrate richness both exhibited significant, and moderately strong negative correlations ($r = -0.225$ and -0.279 , respectively) with macrofungi richness (Table 172, Fig. 67 and 68). Thus, sites richer in fungi tended to have lower richness in bird species and invertebrate families, however relationships were not strong enough to have any predictive value. These relationships were reflective of their respective relationships with channel gradient and large logs

(positive with fungi, negative with birds and invertebrates), and meadow and the forest to meadow gradient (negative relationship with fungi, positive with birds and invertebrates) (Table 173). Additionally, bird richness and fungi richness had opposing relationships with snags and logs (including individual variables and the snag and log gradient), the elevation–precipitation gradient, and subalpine vegetation. Invertebrate richness and fungi richness had additional opposing relationships with alder–willow.

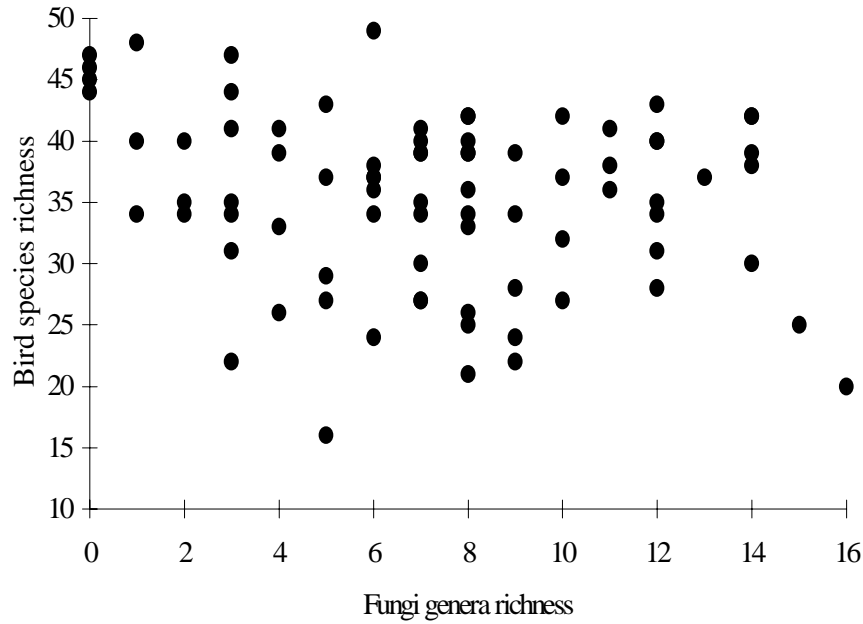


FIG. 67. Relationship between macrofungi genera richness and bird species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

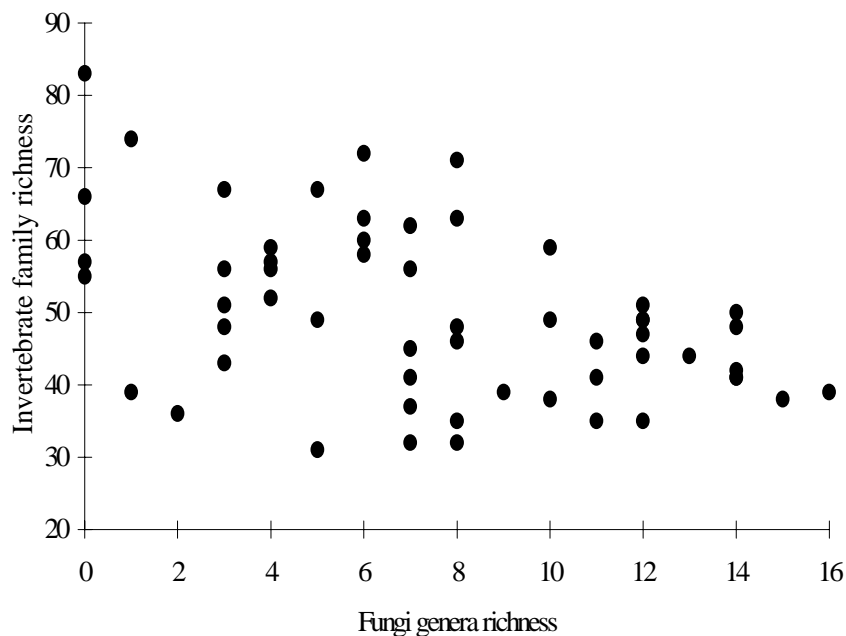


FIG. 68. Relationship between macrofungi genera richness and invertebrate family richness at sample reaches ($n = 56$) in the Lake Tahoe basin.

In addition to interrelationships among the 5 major taxonomic groups, I looked at the relationship of the richness of 3 taxonomic subgroups analyzed in the previous chapters (i.e., Lepidoptera genera, fleshy fungi genera, and lichen genera) with the richness of other taxonomic groups. Many significant correlations were observed among subgroups that were not detected between the 5 primary taxonomic groups; however scatter plots revealed that these relationships were quite variable and would not be useful in a predictive capacity (Fig. 69 to 73). While, invertebrate family richness did not show a relationship with plant species richness, Lepidoptera richness was positively correlated with plant species richness ($r = 0.270$, $P = 0.044$) (Fig. 69). The 2 reaches with the highest plant species richness did not have the highest Lepidoptera genera richness, but a general pattern of mutual increase was still apparent. Similarly, while fungi richness did not show a relationship with plant species richness, fleshy fungi richness was negatively correlated ($r = -0.230$, $P = 0.040$) with plant species richness (Fig. 70). While fungi and invertebrate richness were not correlated, invertebrate family richness was negatively correlated with lichen richness ($r = -0.405$, $P = 0.002$) (Fig. 71). Finally, while no relationships were observed between mammal and fungi richness, fleshy fungi richness was negatively correlated ($r = -0.210$, $P = 0.062$) and lichen richness was positively correlated ($r = 0.197$, $P = 0.080$) with mammal richness (Figs. 72 and 73, respectively).

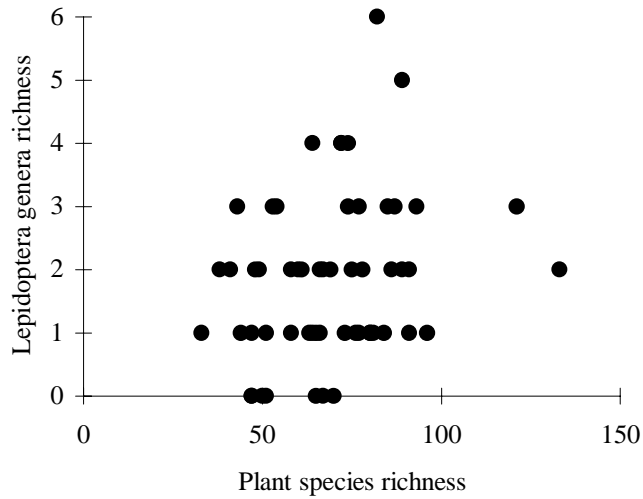


FIG. 69. Relationship between plant species richness and Lepidoptera genera richness at sample reaches ($n = 56$) in the Lake Tahoe basin.

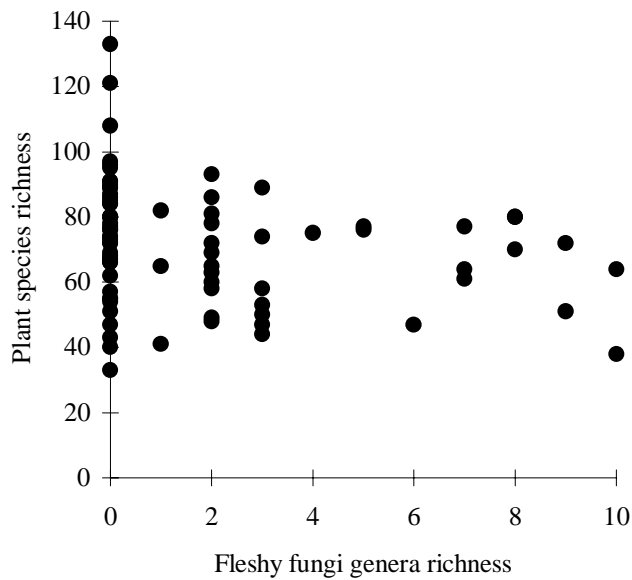


FIG. 70. Relationship between fleshy fungi genera richness and plant species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

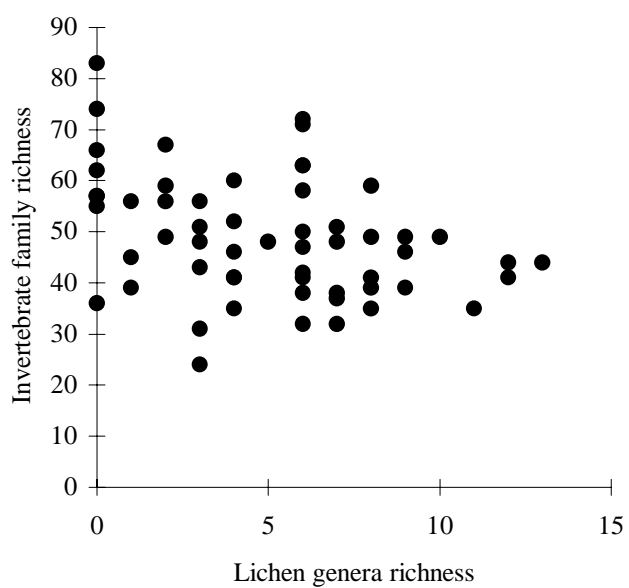


FIG. 71. Relationship between lichen genera richness and invertebrate family richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

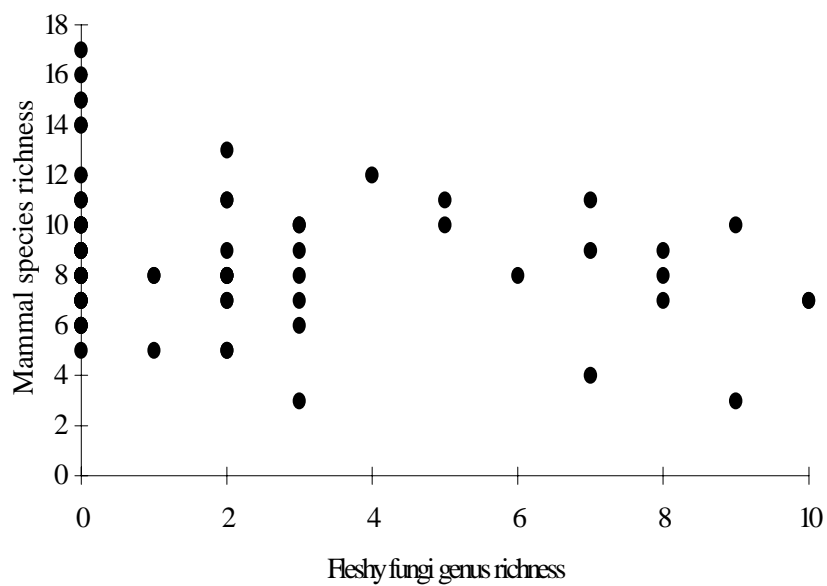


FIG. 72. Relationship between fleshy fungi genera richness and mammal species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

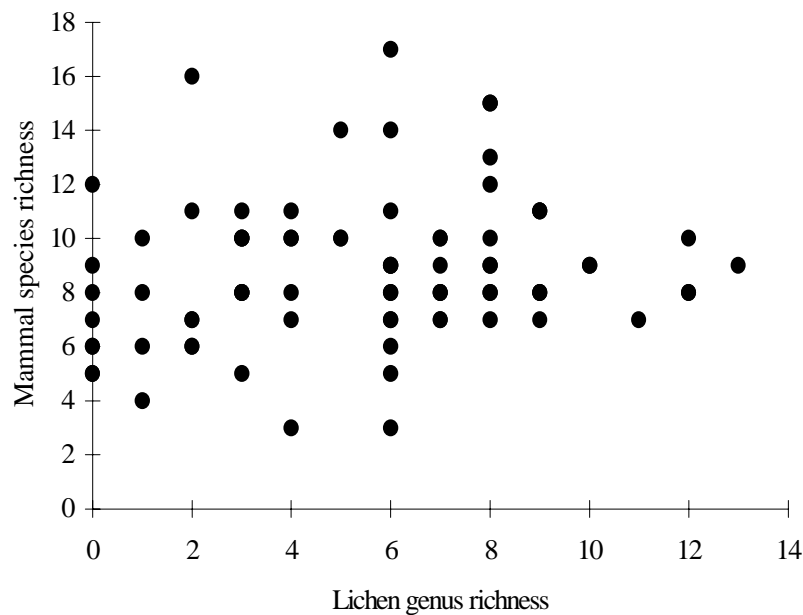


FIG. 73. Relationship between lichen genera richness and mammal species richness at sample reaches ($n = 80$) in the Lake Tahoe basin.

Concordance in Environmental Relationships

A few environmental variables showed strong associations across taxonomic groups. Meadow was correlated with the richness of 4 out of the 5 taxonomic groups (mammals being the exception) (Table 173). The correlations of the richness of 3 taxonomic groups (birds, invertebrates, and fungi) with meadow were 0.40 to 0.50, with plant species richness being a fourth group with a lower but still significant correlation of 0.25. Bird and plant richness were positively correlated with meadow, whereas invertebrate and fungi richness were negatively correlated with meadow. Large or small logs were correlated with one or more of the taxonomic groups. Logs were infrequent in meadows compared to forested environments, and the relationships between richness and logs were the opposing sign of those observed for meadows and richness. The correlations between richness and large or small logs was lower than for meadow, where correlations between logs variables and the richness of most taxonomic groups ranging from 0.20 to 0.30. Lodgepole pine was correlated with all but mammal richness, correlations were positive except in relation to fungi richness, and correlation coefficients ranged from approximately 0.20 to 0.30. Channel gradient was correlated with bird, vascular plant, and fungi richness, with coefficients ranging from approximately 0.38 for bird richness to 0.53 for fungi richness. All but 2 of the remaining environmental variables, were correlated with only 1 or 2 taxonomic groups; shrubs and channel logs were not correlated with the richness of any of the taxonomic groups (although shrubs were selected for one regression model).

The most closely related environmental variables varied among taxonomic groups. Moisture and microclimatic factors (i.e., precipitation and aspect, respectively) were associated with plant richness to a greater degree than other taxonomic groups; however, plant richness was also closely related to meadow and lodgepole pine. Bird richness was also associated with moisture and temperature (i.e., precipitation and elevation, respectively), but was also associated with a range of environmental factors, including channel (primarily gradient), and vegetation (primarily meadow) features. Mammal richness was mostly associated with elevation and rare or special habitat elements, namely aspen–cottonwood and coarse woody debris. Invertebrates and

fungi showed no association with abiotic features and were primarily associated with channel and vegetation features. Invertebrate richness was largely associated with alder–willow and meadow vegetation, but also exhibited a relatively strong relationship with channel gradient. Fungi richness was largely associated with channel gradient, which is likely to be simply a function of the vegetation associations of fungi richness, namely closed-canopied forests, subalpine conifer, and snags.

The adjusted R^2 values for final multiple regressions can serve as one index to the ability of this “generic” set of environmental variables to address conditions relevant to the biological diversity of multiple taxonomic groups. The majority of variation in the richness of each taxonomic group was not explained by relationships with the environmental variables analyzed (Table 174). Although correlation coefficients between richness measures and individual environmental variables were often between 0.40 and 0.50, only once did the adjusted R^2 for multiple regression analyses exceed 0.40 (invertebrate family richness). The remaining adjusted R^2 values ranged from 0.217 for plants to 0.385 for fungi.

TABLE 174. Adjusted R^2 values for final multiple regressions between the richness of each taxonomic group and 22 environmental variables.

Taxonomic group	Final multiple regression adjusted R^2
Birds	0.325
Mammals	0.256
Invertebrates	0.404
Plants	0.217
Fungi	0.385

Beta Diversity

The relative contributions of environmental gradients to turnover (beta diversity) across taxonomic groups were assessed by comparing average values for the modified Whittaker’s index, and comparing rank values for beta diversity. Values for Whittaker’s index of turnover did not vary significantly among gradients across all taxonomic groups (ANOVA, $P = 0.952$). In contrast, average turnover did vary significantly among taxonomic groups across all gradients ($v = 4, 35$; $SS = 0.087, 0.028$; $MS = 0.022, 0.001$; $F = 27.571, P < 0.001$), indicating that some taxa had inherently higher turnover rates than others. Based on Tukey’s test, vascular plants showed greater turnover than birds, mammals, and invertebrates. Further, fungi and invertebrates exhibited greater turnover than birds and mammals, and mammals had significantly greater turnover than birds (based on Tukey’s test). Beta diversity index values did not vary similarly across gradients for any taxonomic groups. Although variation in turnover was greater within than among gradients, turnover did contribute to the diversity of taxonomic groups, and some gradients were influential across multiple taxonomic groups. For example, alder–willow and elevation had the highest average turnover values across all gradients, followed by precipitation, channel flow, and aspen–cottonwood (Table 175).

TABLE 175. Average beta diversity index values (modified Whittaker's index) for each environmental gradient for each taxonomic group.

Environmental gradient	Taxonomic group					Average
	Birds	Mammals	Invertebrates	Plants	Fungi	
Elevation	0.082	0.134	0.163	0.236	0.189	0.161
Precipitation	0.068	0.084	0.180	0.198	0.261	0.158
Channel flow	0.093	0.123	0.184	0.214	0.171	0.157
Forest to meadow	0.072	0.111	0.124	0.206	0.112	0.125
Subalpine vegetation	0.080	0.107	0.181	0.208	0.132	0.142
Alder–willow	0.075	0.146	0.188	0.208	0.204	0.164
Aspen–cottonwood	0.083	0.104	0.171	0.189	0.234	0.156
Snag and log	0.084	0.104	0.147	0.215	0.128	0.136
<i>Average</i>	<i>0.080</i>	<i>0.114</i>	<i>0.167</i>	<i>0.202</i>	<i>0.179</i>	

The average rank value for environmental gradients ranged from 2.8 for the channel flow gradient to 6.6 for the forest to meadow gradient (Table 176). An analysis of variation in ranks within and among gradients revealed that, despite a sizable range in average ranks sums, variation in ranks was greater within than among gradients (ANOVA, $P = 0.146$). This indicates that no one gradient had a greater contribution to turnover than another across all taxonomic groups. Based on rank values, channel flow, alder–willow and elevation were again associated with the highest turnover across all taxonomic groups. These 3 gradients constituted the major contributors to beta diversity in the basin. One or more of these 3 gradients ranked in the top 3 gradients for every taxonomic group, and one of them was the highest ranked gradient for every taxonomic group except fungi. All other gradients had substantially higher average rank values. Finally, ranks did not vary similarly across gradients for any of the taxonomic groups.

TABLE 176. Rank values for 8 gradients relative to beta diversity for each of 5 taxonomic groups. A rank of 1 indicates the highest beta diversity and 8 indicates the lowest beta diversity.

Environmental gradient	Taxonomic group					Average
	Birds	Mammals	Invertebrates	Plants	Fungi	
Elevation	5	2	6	1	4	3.6
Precipitation	6	8	3	7	1	5.0
Channel flow	1	3	2	3	5	2.8
Forest to meadow	8	5	8	5	7	6.6
Subalpine vegetation	4	6	4	6	8	5.6
Alder–willow	7	1	1	4	3	3.2
Aspen–cottonwood	2	7	5	8	2	4.8
Snag and log	3	4	7	2	6	4.4

In addition to total taxonomic change, variation in the proportion of change in species composition attributed to turnover (i.e., turnover/total) occurring between the lower and upper half of each gradient for each taxonomic group was assessed (Table 177). The proportion of change attributed to turnover from the lower to upper halves of each gradient for each taxonomic

group did not vary significantly among environmental gradients (ANOVA, $P = 0.402$), however subalpine vegetation had much higher average beta diversity than any other gradient, followed by alder–willow and aspen–cottonwood. However, proportion of change attributed to turnover did vary among taxonomic groups ($v = 4, 35$; $SS = 0.669, 1.079$; $MS = 0.167, 0.031$; $F = 5.423, P = 0.002$). Multiple comparisons (Tukey’s test) of taxonomic groups showed that birds had significantly lower proportion of total change attributed to turnover than invertebrates and plants, and that mammals had a significantly lower proportion of total change attributed to turnover than invertebrates. These results indicate that birds and mammals were more similar in their composition from site to site than the 2 taxonomic groups with the highest richness. The proportion of change attributed to turnover was not correlated among taxonomic groups.

TABLE 177. Proportion of taxonomic change attributed to turnover between lower and upper halves of each of 8 environmental gradients for 5 taxonomic groups.

Environmental gradient	Taxonomic group					Average
	Birds	Mammals	Invertebrates	Plants	Fungi	
Elevation	0.33	0.30	0.77	0.73	0.50	0.53
Precipitation	0.24	0.29	0.70	0.53	0.46	0.44
Channel flow	0.50	0.22	0.78	0.44	0.67	0.52
Forest to meadow	0.38	0.67	0.43	0.48	0.35	0.46
Subalpine vegetation	0.60	0.80	0.97	0.92	0.50	0.76
Alder–willow	0.36	0.40	0.76	0.92	0.67	0.62
Aspen–cottonwood	0.17	0.60	0.61	0.77	0.90	0.61
Snag and log	0.50	0.33	0.67	0.75	0.67	0.58
<i>Average</i>	<i>0.39</i>	<i>0.45</i>	<i>0.71</i>	<i>0.69</i>	<i>0.59</i>	

Gamma Diversity

The relative contributions of alpha and beta diversity to gamma diversity were explored by reviewing the number of taxa observed per site relative to the total number of taxa observed across all sample reaches (Table 178). The average proportion of taxa observed per site ranged from 0.133 to 0.350, never exceeding approximately one-third of all taxa within the study area. This indicates that between-site diversity (i.e., beta diversity) is responsible for approximately 65 to 85% of the biological diversity in the basin. No correlation existed between taxonomic richness and the proportion of taxa observed per sample reaches ($P = 0.525$). Although vascular plants showed the highest average alpha diversity, birds had the highest proportion of all taxa observed per site, followed by mammals and invertebrates. Vascular plants and fungi had the lowest proportion of taxa observed per sample reach (Table 178).

TABLE 178. Proportion of all taxa observed per sample reach for 5 taxonomic groups.

Taxonomic group	Number of taxa	Average number of taxa per sample reach	Average proportion of taxa observed per sample reach
Birds	101	35.3	0.350
Mammals	35	8.8	0.258
Invertebrates	203	49.9	0.246
Vascular plants	470	71.2	0.151
Fungi	55	7.3	0.133

The contributions of each gradient to gamma diversity in the basin across all taxonomic groups were compared by calculating the percent of all taxa that shifted from the lower to upper half of each gradient (Table 179). The percent of taxa shifting along each gradient did not vary significantly among gradients across all taxonomic groups (ANOVA, $P = 0.553$), indicating that no one gradient influenced a higher proportion of taxa across multiple taxonomic groups than another. Nevertheless, gradients with the highest average values indicate gradients that affected the greatest proportion of taxa. Forest to meadow had the highest average percent of all taxa affected (22.1%), followed by the channel flow, precipitation, and elevation (Table 179). In contrast, variation in the percent of taxa affected varied significantly among taxonomic groups across all gradients ($v = 4, 35$; $SS = 569.95, 399.22$; $MS = 142.49, 11.41$; $F = 12.49, P < 0.001$), indicating that some taxa had inherently greater variation among sites than others. Specifically, vascular plants showed the highest percent change along gradients, and plants and fungi showed significantly greater percent change along gradients than birds, invertebrates and mammals (based on Tukey's test). Finally, invertebrates and plants showed similar shifts in the proportion of taxa changing across gradients ($r = 0.742, P = 0.035$).

TABLE 179. Percent of all taxa shifting (gains, losses, turnovers) along environmental gradients.

Environmental gradients	Taxonomic Group					<i>Average</i>
	Birds	Mammals	Invertebrates	Plants	Fungi	
Elevation	17.8	20.0	15.3	23.6	25.9	20.5
Precipitation	16.8	20.0	18.2	28.1	24.1	21.4
Channel flow	13.9	25.7	18.2	27.9	22.2	21.6
Forest to meadow	12.9	17.1	21.7	27.2	31.5	22.1
Subalpine vegetation	9.9	14.3	14.8	19.6	25.9	16.9
Alder-willow	13.9	14.3	16.7	18.9	22.2	17.2
Aspen-cottonwood	17.8	14.3	17.7	23.0	18.5	18.3
Snag and log	11.9	17.1	19.2	21.7	22.2	18.4
<i>Average</i>	14.4	17.9	17.7	23.8	24.1	

DISCUSSION

Environmental Influences on Biological Diversity

Despite major differences in the life histories and habitat associations within and among taxonomic groups, the same set of macro- and meso-scale environmental variables were effective in describing environmental relationships and patterns of diversity across multiple taxonomic groups. Environmental variables explained 22% to 40% of the variation in richness of individual taxonomic groups, and correlations with individual variables ranged as high as 53%.

Taxonomic groups often had opposing relationships with environmental features. Opposing relationships with 2 or more taxonomic groups were observed in association with meadows, conifer forests, elevation, and precipitation. For example, bird and invertebrate richness were closely associated with meadow and lodgepole pine forests, whereas fungi richness was associated with mixed conifer and subalpine conifer forests. Birds were richer at lower elevations, whereas mammals were richer at higher elevations. Finally, plants were richer, whereas birds were less rich, in association with precipitation, and fungi richness did not change in relation to precipitation but turnover was high.

Environmental features associated with the diversity of multiple taxonomic groups indicate strong drivers of biological diversity in the Lake Tahoe basin. In regard to environmental gradients, none had a significantly greater influence on gamma diversity across all taxonomic groups than any other; variation in turnover rates among taxa was so high that it masked differences in diversity among gradients. However, a few gradients were consistently associated with higher diversity. Channel flow, forest to meadow, and precipitation gradients had the greatest influence on both richness and turnover for many taxonomic groups. Channel flow reflects shifts from upland to aquatic conditions, the forest to meadow gradient reflects the diversity of vegetation types and structures occurring among low to mid elevation reaches, and the precipitation gradient represents a range of moisture availability including the prevalence of aquatic environments. The majority of diversity in lotic riparian biota in the Lake Tahoe basin lies along these 3 environmental axes.

Across all taxonomic groups and environmental gradients, richness and turnover made similar contributions to diversity, with turnover being responsible for an average of 57% and richness responsible for an average of 43% of overall taxonomic diversity. However, this average represents wide variation in the role of richness and turnover in the diversity of each taxonomic group. Birds and mammals had much higher richness per reach and lower turnover rates among reaches than the other 3 taxonomic groups, indicating that neither taxonomic group was highly spatially variable. It appears that taxonomic groups had inherently different between-site variance in species composition. Further, environmental gradients associated with the highest turnover were different from those associated with the highest richness, across taxonomic groups, as well as within them. Thus, richness and turnover not only described different facets of diversity, but they also reflected different progenitors of diversity. For example, meadow and logs were strongly associated with richness for many taxonomic groups, but across all taxonomic groups turnover was generally low along these and associated gradients (e.g., forest to meadow gradient). These results highlight the important contributions that alpha and beta diversity can make to the diversity of an area, and that management based on richness or turnover alone may not be satisfactory in supporting the native diversity of an area.

Interactions Among Taxonomic Groups

The many relationships observed among taxonomic groups reflected similarity in their environmental associations, as opposed to interrelationships between taxa. For example, mammals, plants, and lichen richness were all generally positively correlated with one another, and they all appeared to be responding to denser forest conditions (i.e., mixed conifer and subalpine conifer forests). Further, bird, invertebrate, and fleshy fungi richness were all generally positively correlated with one another, and they all appeared to be responding to more open environments (i.e. meadows and lodgepole pine forests).

A few inter-taxonomic correlations potentially reflected interrelationships. For example, it is plausible that the increase in bird species richness associated with increased invertebrate family richness reflects a response to increased invertebrate food availability. Most song birds rely on invertebrates for some portion of their diet, and may be responding to invertebrate biomass. If birds are at least partly responding to richness of invertebrates, then the environmental features associated with invertebrate richness (i.e., such as meadow and lodgepole pine) may have the potential to indirectly affect bird species richness.

Similarly, higher Lepidoptera genera richness was associated with plant species richness, which could reflect an interrelationship between butterflies and plants. Butterflies and moths are typically stenotypic in their plant species associations, and some are associated with only one plant species (Garth and Tilden 1986), so it is likely that plant species richness would support a greater variety of butterfly and moth species. Other studies have shown positive correlations

between butterfly richness and plant species richness (e.g., Thomas and Mallorie 1985, Murphy and Wilcox 1986). My results indicate that this relationship can be expressed at the genus level for Lepidopterans. The fact that Lepidoptera richness showed virtually no relationships with any of the environmental features analyzed lends further credence to the notion that the observed relationship between Lepidoptera and plant richness is not an artifact of related environmental features.

Despite moderately strong correlations in the richness of some taxonomic groups, individual taxonomic groups were not good predictors of the diversity of other taxonomic groups. Greater variation in diversity among taxonomic groups versus among gradients, and the large proportion of variation (over 70%) unexplained in correlations between any 2 taxonomic groups provides evidence of the inadequacy of any one taxonomic group's ability to represent the richness and diversity of other taxonomic groups.

Conservation and Management Implications

The conservation of biological diversity in a geographic area is typically motivated by the area being unusually diverse, unique, ecologically intact, highly aesthetic, or otherwise of high social value. The Lake Tahoe basin is a unique environment within the Sierra Nevada, and it is of high social value because of its beauty and environmental diversity. Thus, the conservation of biological diversity in the basin is of great interest, but it is not the primary feature that confers such high social value to the basin. My study served to highlight the significant contribution of lotic riparian environments to the support of biological diversity in the Lake Tahoe basin, and to illustrate that elucidating relationships between diversity and environmental features can yield a plethora of information valuable to the conservation and management of biological diversity in the basin. The first step toward conserving biological diversity in an area such as the Lake Tahoe basin is to understand (to the extent possible) the conditions that support a full suite of native biota. The second step is to then apply this understanding to the design and implementation of a conservation strategy to maintain and restore biological diversity.

Ecological Conditions Supporting Biological Diversity

It is not surprising that channel geomorphology would have a strong influence on biota proximal to streams (Gregory et al. 1991, Naiman et al. 1993); however few studies target geomorphology for study in investigations of as riparian associated biota (e.g., Burnett et al. 1998, Nichols et al. 1998). Results of my study showed that biological diversity in stream-side environments is strongly responding to abiotic, meso-scale environmental features associated with channel characteristics. It is noteworthy that between the effects of channel gradient, width, and sinuosity, the richness of every taxonomic group was affected in some manner by channel flow characteristics. Conservation and restoration efforts focused on in-stream conditions and biota should take into consideration the potential impact they may have on riparian-associated biota.

Many studies have demonstrated that taxonomic richness is affected by elevation and associated climatic conditions (e.g., Terborgh 1971). In particular, conditions that favor biological production in terrestrial environments (i.e., warm temperatures and abundant precipitation) are often associated with high diversity (Schluter and Ricklefs 1993). However, I found that precipitation and elevation (to a lesser degree) were associated with high levels of turnover, and had opposing relationships with richness of birds, mammals, and plants. Although management does not typically affect precipitation over short time periods, the relationship between diversity, precipitation, and elevation has management implications in terms of being important gradients to be represented in areas identified for the conservation of biological diversity in the Lake Tahoe basin.

Meadows supported a rich and diverse array of taxa. Given that meadow occurred on less than half of the sample reaches, it is clear that meadows play an important role in supporting biological diversity in the Lake Tahoe basin, and that meadow management alone could substantially affect biological diversity. Wet meadows in an upper montane and subalpine environment must provide a unique and rich array of resources for all but the most stenotypic forest associates. A greater diversity of plants, in addition to birds and invertebrates, would potentially result from an increase in the quality and quantity of meadows in the basin. Most lichen genera and certain mammal species (e.g., Douglas squirrel, golden-mantled ground squirrel) were some of the few taxa that would not benefit directly from managing meadows for biological diversity.

Potential threats to the quality and quantity of meadows include grazing, lack of fire, and channel restorations. Most meadows in the Lake Tahoe basin are currently grazed by cattle, and even a moderate level of grazing may have deleterious effects on many species, including ground and shrub nesting birds, meadow-associated small mammal species, larger-bodied grazing and browsing mammal species, and amphibians (Cooperrider 1991, Fleischner 1994). Deleterious effects from grazing may be reduced by invoking seasonal restrictions on grazing in meadows with the highest potential for supporting high biological diversity, however some studies suggest that grazing must be eliminated for some period of time to effectively restore meadow function (Dahlem 1979, Chaney et al. 1990). Fire strongly influences the function and maintenance of meadows in the Sierra Nevada (Ratliff 1985). Agencies within the Lake Tahoe basin are increasing the use of prescribed fire in an attempt to restore the function of fire in reducing flammable fuels. The planned increased use of prescribed fire in the basin should improve the quality and quantity of meadows if burns are light such that soil moisture conditions are not altered (Ratliff 1985). Channel restoration could affect meadow conditions, as well as alder and willow abundance. Restoration efforts that involve key meadow complexes with well-developed alder and willow vegetation should be carefully considered so as to avoid detrimental effects on riparian and meadow environments.

The high value of lodgepole pine to taxonomic richness is in contrast to generally held perceptions (e.g., Verner and Boss 1980) that lodgepole pine stands provide habitat for relatively few species because of their structural simplicity. Duality of this species' life history, growing both in mesic environments and high, xeric elevation sites may be responsible for this apparent contrast. In this study, all lodgepole pine stands sampled were in mesic environments in association with streams. It is possible that these lodgepole pine stands offer a rich array of resources and conditions favorable to a diversity of biota compared to the high, xeric elevation lodgepole pine stands. Potential management impacts include cattle grazing and fire management, and an assessment of the interaction of grazing and fire with key features of lodgepole pine stands would provide valuable insights into how best to manage lodgepole pine stands to conserve biological diversity.

Riparian woodland vegetation, namely alder–willow and aspen–cottonwood, contributed to the support of a diversity of biota in the Lake Tahoe basin. Aspen–cottonwood had a positive influence on the richness of birds and mammals, and alder–willow had a positive influence on the richness of plants and invertebrates. Both vegetation types were associated with turnover for 3 or more of the 5 taxonomic groups. The management of these vegetation types will substantially affect the diversity of most macrobiota using stream-side riparian areas in the basin. Conservation efforts should not assume that more alder–willow and aspen–cottonwood will necessarily enhance biological diversity, but rather they are important gradients to be represented in areas identified for the conservation of biological diversity in the Lake Tahoe basin. Further, the quality of alder–willow and aspen–cottonwood could be affected by management activities such as grazing, fire management, and channel restoration.

The varied interrelationships of richness among taxonomic groups provide insights into how best to design conservation approaches. The richness of birds, invertebrates, and fleshy fungi all followed similar patterns in association with environmental features, and were closely associated with more open-canopied environments, particularly meadows. Conversely, the richness of mammals, plants, and lichen were all similarly associated with more upland, forested environments. Conservation of meadow environments, for example, should take into consideration the array of closely associated biota and general considerations in support of their diversity.

Monitoring Biological Diversity

A growing number of studies have investigated the potential of the diversity of one species group to represent the diversity of a wider array of species, essentially serving as indicators of diversity (e.g., Murphy and Wilcox 1986, Pharo et al. 1999). For example, Murphy and Wilcox (1986) suggested that plant species richness may serve as an adequate surrogate for butterfly richness in the mountains of Nevada. However, many studies have concluded, as I have, that although correlations in diversity do exist between some species groups, the relationships rarely correspond closely enough to serve as useful indicators for one another (e.g., Wylie and Currie 1993, Robbins and Opler 1997, Patterson et al. 1998, Pharo et al. 1999). Thus, the potential of greatly simplified environmental inventory or monitoring efforts through the employ of indicator species groups does not appear to be a viable option in the Lake Tahoe basin. To the contrary, changes in patterns of richness among taxonomic groups provide valuable insights into the biotic and abiotic processes driving changes (or lack thereof) in biological diversity within and among taxonomic groups. They also represent a greater array of ecological diversity (the variety of ecological roles, diet components, and microhabitat uses exhibited by an assemblage of species) and morphological diversity (the variety of physical characteristics of species) (see Ricklefs and Miles 1993 for discussion), which can be mined through analysis to gain additional information on trends in diversity and insights into the environmental factors driving observed trends.

Differences among taxonomic groups in their associated environmental features indicate that one or even a few environmental features would not be sufficient indicators of biological diversity across taxonomic groups. For example, vegetation types are often used as a surrogate for describing potential habitat for species, particularly vertebrates and invertebrates (e.g., Powell and Hogue 1979, Airola 1988). In riparian environments in the Lake Tahoe basin, it was clear that taxonomic groups were responding to a variety of environmental features, both biotic and abiotic. The distribution and abundance of vegetation types did not track patterns of variation for other biotic and abiotic environmental features that surfaced as major influences on biological diversity. It is still possible that indicators of richness and diversity could be found or developed, but data collection and analysis would have to be structured to specifically query for sufficiently robust relationships.

Two potential measurement biases were identified in this study as important considerations in sampling multiple taxonomic groups to assess patterns of biological diversity, either in the context of a survey or for the purposes of monitoring. First, richness measures can mask trends in richness depending on how they are analyzed. The interface of alpha and beta diversity lies at the scale at which spatial variation is described. In this study, spatial variation was described at one primary scale, that is between segments along the length of each environmental gradient. Spatial variation within each segment was not a focus of this study, but for the most speciose taxonomic group (plants), within-segment variation revealed differences in richness along the gradient that were not revealed at the reach scale. Analyses addressing both alpha and beta diversity rarely employ more than one scale of analysis for beta diversity, however valuable information on the patterns of diversity could be lost or mis-interpreted by a single scale of analysis for beta diversity.

The second potential measurement bias involves differences in detectability among taxonomic groups, which can affect the proportion of taxa observed per site. For example, plants had the highest variability among sites, and their overall high richness and breadth of specializations are probably responsible for their variability. Invertebrates also had relatively high inter-site variability, and, like plants, it is likely that their high richness and specialization are responsible for their variability. However, the high inter-site variability observed for fungi is likely to be a combination of the difficulty in censusing this group, as well as their tremendous diversity which is not adequately represented in the range of genera detected. It is unavoidable that observers will miss taxa during a survey. Plant and fleshy fungi taxa are notoriously difficult to census because their presence in fruiting-bodies (fungi) or vegetation growth (plants) can occur for short periods of time, and some taxa may not produce fruiting bodies or vegetative growth every year. Some species of birds, plants, and mammals are readily detected because of frequent vocalizations or visually obvious life forms. However, some members of every taxonomic group will be difficult to detect for one or more reasons. Such species (e.g., bats, owls) may require a disproportionate share of available funding if the desire is to equally represent all species in a taxonomic groups. Monitoring efforts attempting to address patterns of diversity across taxonomic groups may be able to develop correction factors for detectability which adjust observed values based on expected values. Expected values could be derived through a variety of field and analysis techniques.

Designing a Conservation Strategy for Biological Diversity

A landscape-scale conservation approach is necessary to address the conservation of multiple taxonomic groups in an area the size of the Lake Tahoe basin. Landscape is defined as a mosaic of habitat patches across which organisms move, settle, reproduce, and eventually die (Forman and Godron 1986). Conservation reserves are a common approach to conserving biological diversity within landscapes (Soulé and Simberloff 1986), and various permutations of their application have been proposed and implemented over the past 20 years (e.g., Pickett and Thompson 1978, Harris 1984, Noss and Harris 1986). Basic considerations in the design of conservation reserves include the following 6 issues: (1) how large should they be (single large or several small), (2) do they encompass the spatial and temporal heterogeneity and dynamics of the landscape (minimum dynamic area), (3) how does the surrounding “matrix” affect the quality of the reserve, (4) are major landscape features connected in a manner that facilitates movement of biota, (5) should landscape features that have been modified be included in the reserve design, and (6) are buffer zones needed or desired around reserves (multiple-use modules) (Janzen 1983, 1986, Harris 1984, Noss 1991, Meffe and Carroll 1997).

The relatively equivalent contributions of richness and turnover to biological diversity in the Lake Tahoe basin indicate the need for a broad, landscape approach to conserving biological diversity in which the majority of the basin is managed with an eye toward the conservation of biological diversity. However, it is not socially desirable nor economically feasible to devote the entire landscape to the primary purpose of conserving biological diversity. Rather, special consideration of the 6 reserve design issues, combined with current human uses and needs, will be required in the design of a strategy to conserve biological diversity in the basin. Barrett and Barrett (1997) proposed the notion of bioreserves, a regionalized network of individual preserves as core sites integrated within a series of concentric zones acting as successive buffers or corridors to the core sites. Bioreserves, analogous to biosphere reserves (UNESCO 1974) and reserve networks (Noss and Cooperrider 1994), could be established in the Lake Tahoe basin based on the environmental features identified as associated with high diversity for one or more taxonomic groups. Buffer areas could be designed based on a balance of societal demands and the vulnerabilities of focal taxa.

The fact that many macro- and meso-scale environmental variables were moderate to strongly associated with the diversity of taxonomic groups suggests that such environmental variables could be used as the basis for the establishment and management of reserves and buffers throughout the Lake Tahoe basin. For taxonomic groups with lower turnover among sites, such as birds and mammals, identifying areas with environmental conditions associated with high richness is likely to provide for the majority of species. Stream lengths with low gradients and wider channel, meadows, and aspen–cottonwood stands would be the targets for bioreserves for the purposes of conserving bird and mammal diversity, with buffers being focused on protecting habitat quality, such as minimizing disturbance to ground-nesting birds. Predictive models could potentially be developed to specifically identify areas of high bird or mammal richness, which could then serve as core areas for bioreserves. Given the large amount of unexplained variation in the diversity of most taxonomic groups, it is advised that conservation strategies be designed to validate and improve upon the current understanding of environmental conditions that support biological diversity in the Lake Tahoe basin.

Taxonomic groups with the highest turnover among sites, such as invertebrates, plants and fungi, are the most challenging to conserve because essentially every site may be important for supporting one or more rarely occurring taxa. The concept of a coarse-filter approach to conservation, developed by the Nature Conservancy (Noss 1987), would apply well in the case of conserving the majority of stream-associated bird species in the Lake Tahoe basin. The coarse-filter approach would entail conserving a breadth of vegetation and aquatic community types without specific attention paid to the species associated with each. In the case of invertebrates, plants, and fungi, the issues of heterogeneity and connectivity become highly relevant. It would be important to encompass the range of biotopes in the basin and their heterogeneity such that bioreserves represented the range of types and conditions in the basin. Buffer size and management might be based primarily on the vulnerabilities and natural disturbance regimes of the biotopes because of the broad array of taxa they were established to support.

Conclusions

My research effort was able to identify distinct patterns of variation in biological diversity within and among diverse taxonomic groups in lotic riparian environments in the Lake Tahoe basin. Although most environmental characteristics I analyzed reflected local environmental conditions, it appeared that larger temporal and spatial scale processes, such as emigration, also influenced the composition of taxonomic groups studied. Environmental features classically associated with productivity, namely as elevation and precipitation, were strongly associated with the diversity of many taxonomic groups in the basin, but their contributions to diversity were as strong in terms of turnover as they were in terms of richness. Apparent increases in productivity were not accompanied by gaining additional taxa, but rather were associated with major shifts in species composition, where some species were lost while others were gained.

Spatial heterogeneity also had a strong influence on the diversity of many taxonomic groups. Channel flow represents a shift from lower to higher productivity and spatial heterogeneity, and had the greatest influence on diversity of any abiotic environmental feature, and affected both richness and turnover. Vegetation types, particularly shifts in vegetative conditions along the forest to meadow gradient, were strongly associated with the diversity of most taxonomic groups. The positive association between meadow and birds and invertebrates appears in contrast with theories of increasing diversity with structural complexity (MacArthur and MacArthur 1961, Pianka 1967), however at a larger geographic scale, the presence of meadow increases the spatial heterogeneity and structural complexity of the landscape.

The investigation of both alpha and beta diversity provided valuable insights into how various environmental features affected biological diversity. I found that alpha and beta diversity were often responding to very different environmental features, and if only alpha or beta diversity had been investigated I would have overlooked features of critical importance in supporting biological diversity in the Lake Tahoe basin. Assessing both alpha and beta diversity appears to provide a sound foundation for designing strategies to conserve biological diversity, particularly where the conservation of many taxonomic groups in a heterogeneous environment is of interest.

The conservation of biological diversity is a complex undertaking, and the consideration of many taxonomic groups and sources of diversity exacerbates the difficulty of the task. However, it is maintaining and restoring this same complexity that is the ultimate goal of conservation, and grappling with this complexity may be the only means by which conservation efforts have a chance of retaining the function, as well as the presence, of biota in ecological systems (Meyer 1997). Incomplete information will always introduce uncertainty into the assessment of biological diversity and its application to conservation actions. Three main variables which influence uncertainty and risk are (1) the quality, depth, and breadth of information available; (2) the complexity and non-linearity of the processes whose outcomes we are trying to predict; and (3) how far into the future we wish to carry our predictions (Carroll and Meffe 1997). Conservation efforts must proceed despite uncertainties, and continuing research into the environmental factors and biotic interrelationships driving biological diversity can provide valuable new information to improve and enhance conservation efforts. The fate of biological diversity in lotic riparian ecosystems of the Lake Tahoe basin will depend on the ability of agencies and the public to move forward with conservation efforts in the face of imperfect knowledge, and to continue support for efforts to gain better information over time.